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THE MORPHOLOGY AND SYSTEMATIC POSITION OF PODOMITRIUM

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The present classification of the thallose Jungermanniales ("Anacrogynae" of Leitgeb) is very far from satisfactory, as our knowledge of the morphology of several genera is still very fragmentary.

The genus Podomitrium, with which the present paper is concerned, comprises two known species, *P. Phyllanthus* of the Australasian region, and *P. Malaccense*, which Stephani[1] states has been reported hitherto only from Singàpore and New Caledonia. Stephani unites Podomitrium with Umbraculum to form the genus Hymenophytum, but there seems to be ample reason for separating the two genera.

In the spring of 1913 the writer collected at several places in Sarawak, in Western Borneo, abundant material of *P. Malaccense*, which is a common liverwort of this region, and it was also found at a single station in Luzon, Philippine Islands. It is highly probable that the plant will be found in the Southern Philippines also, but, as the sterile plants are indistinguishable from a Blyttia, it cannot be certainly recognized except when fertile.

Podomitrium Malaccense grows upon the ground, usually upon clay soil, and, when it was first collected by the writer, it was supposed to be a species of Blyttia, which it exactly resembles except for the special fertile branches developed from the ventral side of the thallus. In the species under consideration the thallus is usually very unsymmetrical, one wing being almost completely suppressed (figs. 1, *B*; 3, *A*). The conspicuous midrib bears upon its lower surface numerous short rhizoids which are generally in bunches separated by considerable areas nearly or quite bare of rhizoids (fig. 1, *A*).

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[1] Stephani, F. Hymenophytum Malaccense St. Species Hepaticarum—Mém. Herb. Boiss. 11, 1900.

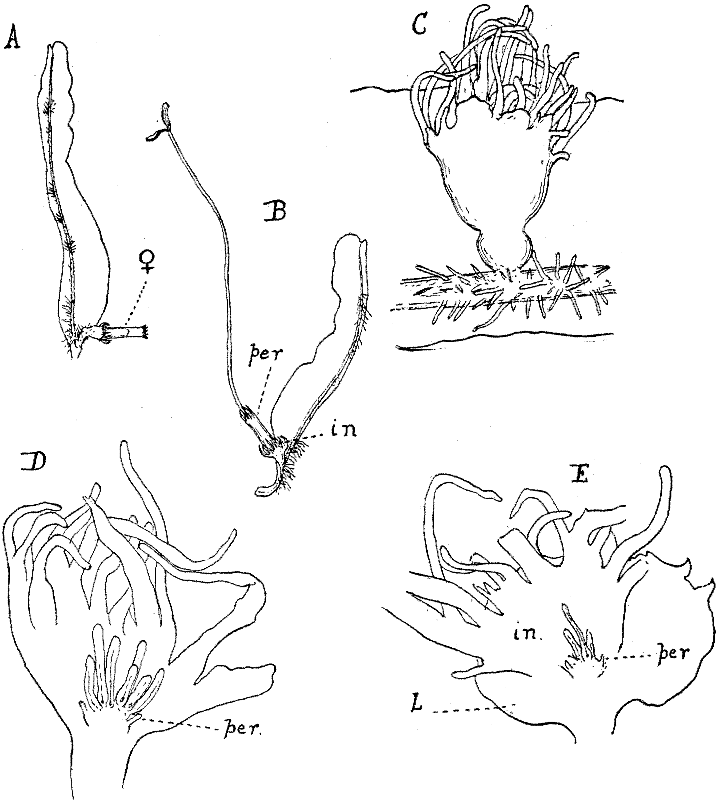

FIG. 1. *A*. Female plant of *Podomitrium Malaccense* seen from below, showing the branch ♀ bearing a young sporophyte, × 2. *B*. A plant bearing a ripe sporophyte which has opened by two free valves; the base of the seta is enclosed in the perianth, *per*, and the involucre, *in*. *C*. A young archegonial branch seen from below, × 16. *D*, *E*. A somewhat older branch split through the middle of the archegonial group—*L*, lamina of the shoot; *in*, the involucre; *per*, the undeveloped perianth.

The anatomy of the thallus is almost identical with that of Blyttia. The clearly defined midrib is composed of several thicknesses of small cells while the lamina has but a single layer of larger cells. Traversing the midrib is a strand of narrow, thick-walled, pitted cells, closely resembling the corresponding tissue in Blyttia (fig. 2, *C*, *D*).

As in other Jungermanniales the growth of the shoot is from a single apical cell which closely resembles that found in most species of Blyttia.[2] It is the common "two-sided" apical cell, with segments cut off successively right and left. In horizonatal section it has the form of a rather narrow isosceles triangle, while in vertical longitudinal section it appears as a nearly equilateral triangle (fig. 2, *A*, *B*).

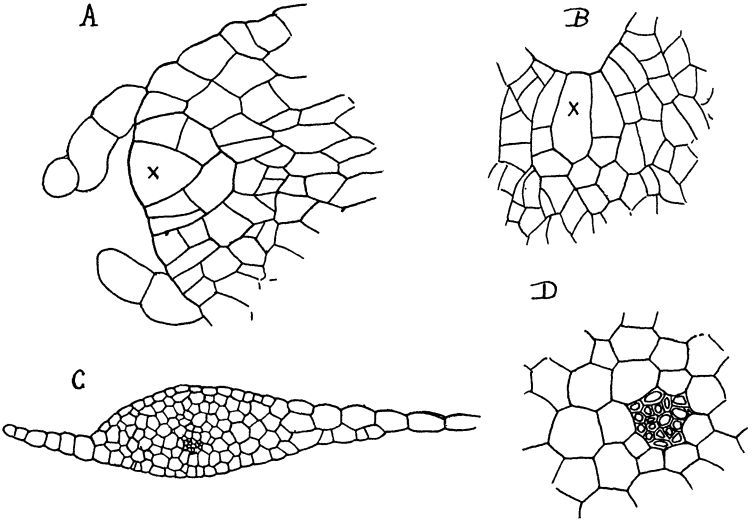

FIG. 2. *A*. Vertical longitudinal section through the apex of the thallus, showing the single apical cell, *x*; × about 300. *B*. Horizontal section of the thallus apex. *C*. Cross-section of the thallus, showing the very unequal wings, and the massive midrib with its strand of conducting tissue; × about 35. *D*. The central region of the midrib; × about 200.

In the position of the sexual organs Podomitrium most nearly resembles Metzgeria in having them borne upon special short branches which arise from the flanks of the midrib upon the ventral side of the thallus. These special fertile branches at once distinguish Podomitrium from Blyttia where both archegonia and antheridia are borne upon the unmodified thallus. The antheridia are borne upon short flattened branches which may be produced on both sides of the midrib of a main shoot, or, in case the lamina of the latter is suppressed, on one side; the antheridial branches are developed from the other side only of the main shoot (fig. 3, *A*).

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[2] Campbell, D. H. and Williams, F. A Morphological Study of Some Member of the Genus Pallavicinia. Stanford University, 1914.

While the antheridia are produced for the most part in two rows corresponding to the two sets of segments cut off from the apical cell some of them may be formed almost in the median line of the shoot, so that an imperfect third row may be present. Each antheridium is covered by a scale with irregularly laciniate margin, and the lamina of the antheridial shoot also has its margins irregularly toothed and lobed (fig. 3, *C*). In the arrangement of the antheridia, *Podomitrium Malaccense* recalls very strongly *Blyttia* (*Mittenia*) *Zollingeri*,[3] and perhaps even more *Calycularia radiculosa* (Sande Lac) Steph.[4]

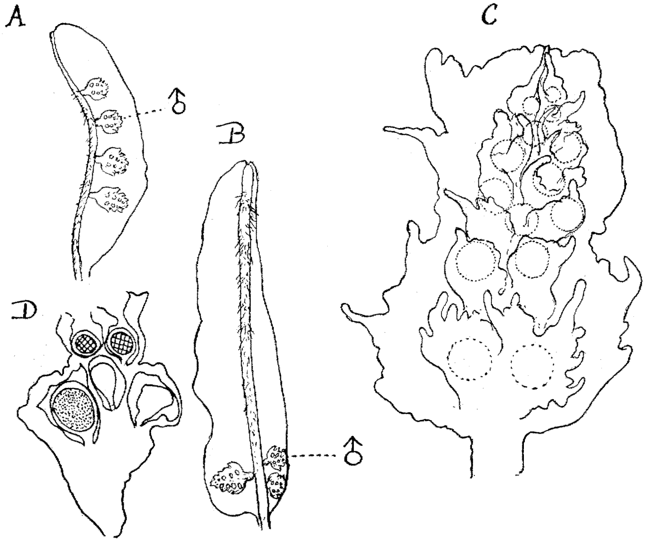

FIG. 3. *A*. Male plant, with the lamina on one side entirely suppressed; ♂, the antheridial branches; × 2. *B*. Male plant with antheridial branches developed on both sides of the midrib. *C*. An antheridial branch, showing the antheridia covered by the subtending scales; × 25. *D*. Horizontal section of a very young antheridial branch, × about 35.

The youngest antheridia occur close to the growing point of the shoot. The beginning of the subtending scale is evident as soon as the antheridium can be recognized (fig. 4, *A*). The development of the antheridium is almost exactly like that of Blyttia, and indeed does not show any marked departure from the type characteristic of the Jungermanniales. The mother-cell of the antheridium divides first

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[3] Campbell and Williams, loc. cit.

[4] Campbell, D. H. The Morphology and Systematic Position of Calycularia radiculosa (Steph.). Reprint from Dudley Memorial Volume, Stanford University, 1913.

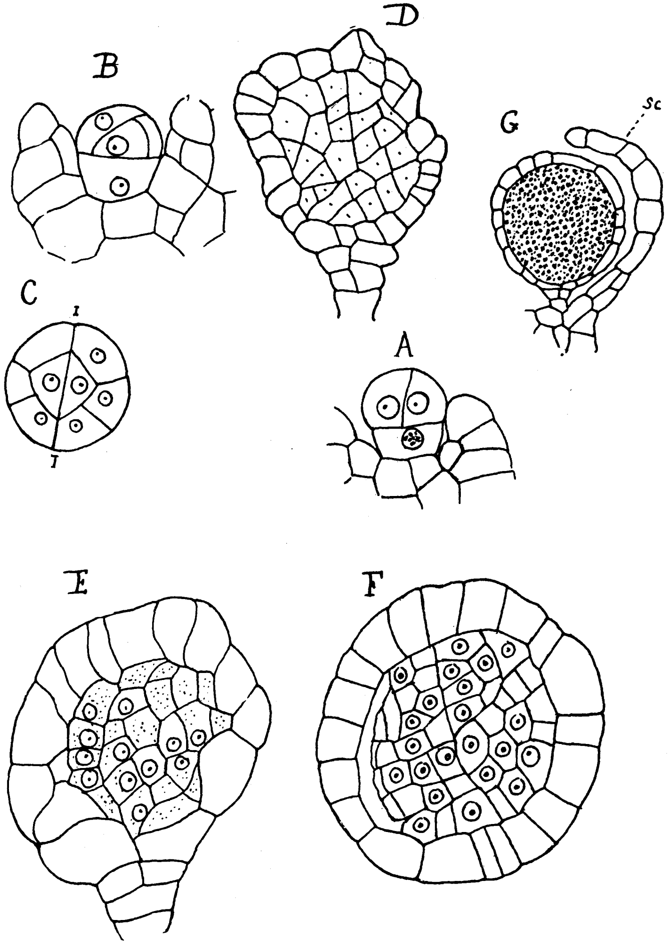

FIG. 4. *A*, *B*. Very young antheridia, seen in longitudinal section. *B* is cut in a plane at right angles to that of *A*; × 335. *C*. Cross-section of a somewhat older stage, × 335; *I–I* the primary median wall. *D*. Nearly median section of an older antheridium. *E*, *F*. Two sections, slightly oblique of an older stage. *G*. Median section of a ripe antheridium, × 75. *sc*, the subtending scale.

into a short basal cell which subsequently divides further to form the short stalk of the older antheridium, and a terminal cell which is nearly hemispherical and develops into the body of the antheridium. This hemispherical cell, as usual in the Jungermanniales, first divides by a vertical median wall, and in each of the two cells thus formed two intersecting walls next arise which separate an inner cell in contact with the original median wall, and two peripheral cells (fig. 4, *B*). In cross section, the pair of central cells, from which subsequently the sperm-cells arise, appear triangular in outline (fig. 4, *C*). As in most other Jungermanniales, the peripheral cells divide by radial walls only, so that the wall of the antheridium remains permanently but a single cell in thickness. The further divisions in the central cells were not followed in detail but the final divisions result in the spermatocytes which are in pairs as has been described in various other Hepaticae. The details of spermatogenesis were not critically studied, as the material did not seem to be especially favorable for this purpose, and there was

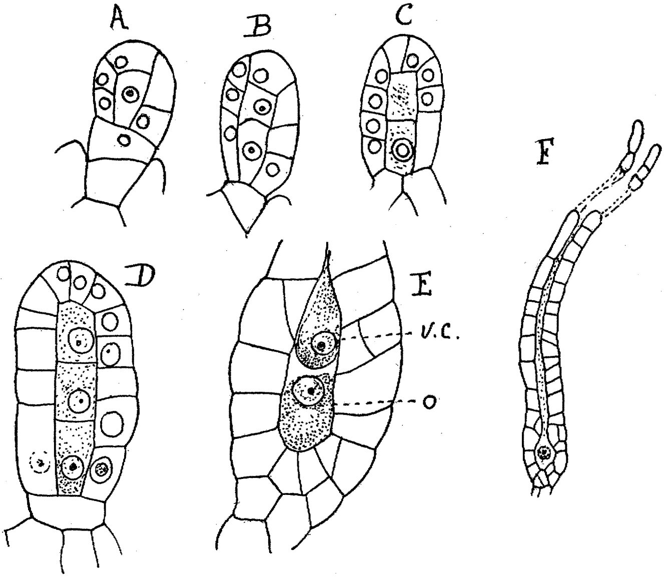

FIG. 5. *A–E*. Development of the archegonium, seen in longitudinal section; × 335. *F*. An old archegonium, which has not been fertilized; × 75. *v. c.*, ventral canal cell; *o*, egg cell.

nothing to indicate any deviation from what has been described for other related forms. The number of chromosomes in the sperm nucleus is eight, the same as has been found in Blyttia.

The archegonia are in a group upon the dorsal surface of short lateral shoots (fig. 1, *C–E*). These archegonial branches are so short that they are almost hidden by the large involucre which surrounds the archegonial group. No midrib is developed in the archegonial shoot which has the form of a thin nearly orbicular lamina with a more or less conspicuously toothed margin. The involucre has its margin composed of numerous slender appendages forming a dense fringe. The archegonia may number a dozen or more in a receptacle, and show different ages in the same group. They are borne upon a more or less evident elevation or placenta. Surrounding each group of archegonia is an inconspicuous elevated ridge or ring—the perianth. Should none of the archegonia be fertilized the perianth remains rudimentary; but, where an embryo is developed, the perianth grows very rapidly and forms a tubular sheath which encloses the growing sporophyte and projects far beyond the involucre (fig. 1, *A*, *B*). The margin of the perianth, like that of the involucre, is conspicuously fringed.

Both involucre and perianth in Podomitrium are very much like those of Blyttia, and, except that the archegonia are produced on special branches, the two genera are scarcely distinguishable. The archegonia themselves (fig. 5) show no marked peculiarities, and are also practically identical in structure with those of Blyttia. There is usually a more or less evident stalk developed, and in the terminal cell of the young archegonium there are formed the usual three intersecting walls cutting out an axial cell from three peripheral cells. From the former the cap cell is now cut off, and this sooner or later divides by quadrant walls into the usual four terminal cells of the archegonium. This division generally takes place somewhat later in Podomitrium than is usual in the Liverworts, and sometimes it looks as if there was a limited apical growth of the young archegonium due to lateral segments cut off from the primary cap cell before its final division by quadrant walls (fig. 5, *D*). In this respect *Podomitrium Malaccense* may be compared with *Blyttia Levieri*[5], where a similar condition has been noted. It also recalls the apical growth in the moss archegonium, although, in the latter, canal cells are also cut off from the basal segments of the cap cell, while such limited apical growth as may occur in Podomitrium and some other Liverworts is confined to the peripheral neck cells.[6]

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[5] Campbell and Williams, loc. cit.

The transverse walls which separate the ventral and neck regions of the young archegonium are formed before any division takes place in the cap cell. The neck may become much elongated, especially when fertilization fails to occur (fig. 5, *F*).

As usual the lower of the primary axial cells divides the egg and ventral canal-cell (fig. 5, *E*), and from the other, by a succession of divisions, the row of neck canal cells is formed. The exact number of the latter could not be made out with certainty, but is probably eight.

In the ventral region, occasional periclinals may form in the peripheral cells, so that at the time of fertilization the wall of the venter is incompletely two-layered (fig. 5, *E*).

THE EMBRYO

Most of the archegonia fail to be fertilized and only a small number of young embryos could be found in the material collected. To judge from the few that were secured, the early divisions seem to resemble very much those in the embryo of Blyttia. Figure 6, *A*, shows the youngest embryo that was found. This was somewhat shrunken but showed an apparent division into two cells by means of an obliquely transverse wall. This first wall is probably followed by one or two more transverse walls before any vertical divisions are formed, but embryos showing these stages were not seen. The basal cell of the young embryo, and probably also the cell above it, give rise to a conspicuous appendage or haustorium, which, however, is not so large as in Blyttia.

Fig. 6, *B*, shows two nearly median longitudinal sections of an older embryo in which all but the lowest of the primary cells had divided by median vertical walls. In the upper regions there were also secondary transverse divisions, but as yet no periclinal walls.

No stages were encountered between the one just described and very much older ones in which the sporogenous tissue was already evident, and it is impossible to say just what is the relation of the different parts of the young sporophyte to the primary divisions of the embryo. It is certain, however, that the basal cell, and probably

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[6] Gayet, L. A. Recherches sur le devéloppement de l'archégone chez les muscinées. Ann. Sci. Nat. Bot. VIII. 3. 1897.

the one above it, contribute only to the haustorium, while all of the sporophyte itself—foot, seta and capsule—arise from the terminal segment, or segments.

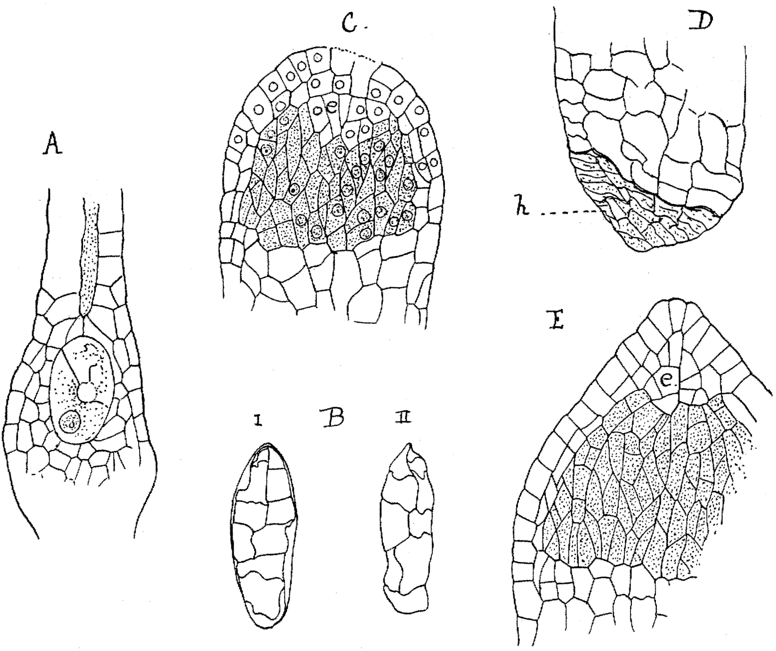

FIG. 6. *A.* Venter of archegonium containing a two-celled embryo; × about 175. *B.* Two sections of an older embryo; × 175. *C.* Upper part of older embryo showing the sporogenous tissue and the elaterophore, *e.* *D.* Base of young sporophyte, showing the remains of the haustorial tissue, *h.* *E.* Upper part of young sporophyte, more advanced than that shown in *C.*

The young sporophyte is almost cylindrical in form, and in the upper part, which is only slightly enlarged, the sporogenous tissue can be readily distinguished (fig. 6, *C*). The capsule wall at this stage is composed for the most part of two layers of cells which are decidedly larger in the apical region. Below the apex is a group of cells belonging to the sporogenous region which differ from the true sporogenous tissue in having less dense contents. This sterile mass of potential sporogenous tissue is evidently the homologue of the elaterophore found in Aneura and Metzgeria, and in this respect Podomitrium differs from Blyttia which it otherwise closely resembles. At this stage a definite foot cannot be distinguished, but the lower part of the stalk is occupied by a comparatively large mass of cells (fig. 6, *D*, *h*) which are partially disorganized, and probably represent the remains of the haustorium; but whether all of these cells are derived from the division of the one or two primary haustorial cells, could not be determined.

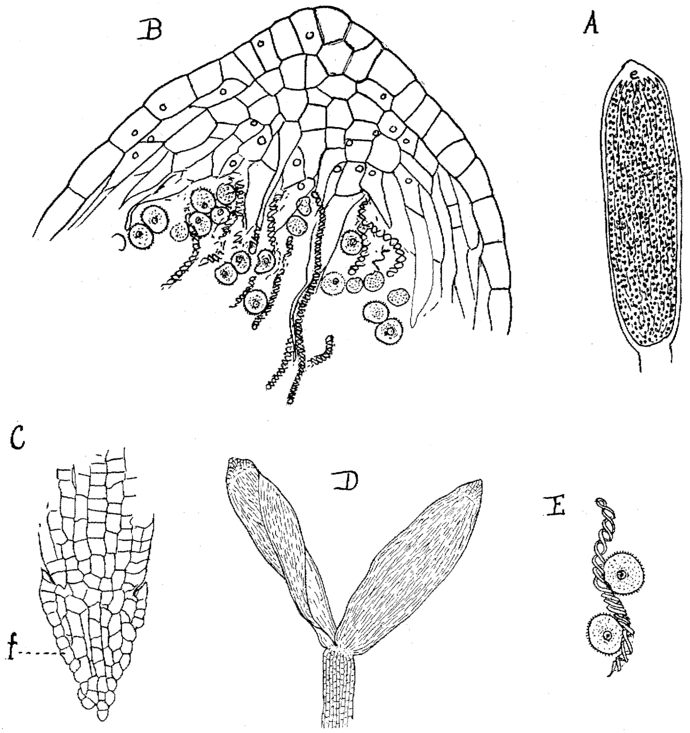

FIG. 7. *A*. Median section of a ripe capsule; *e*, elaterophore; × about 16. *B*. Upper part of the same more highly magnified. The lower cells of the elaterophore are much elongated. *C*. Foot of a nearly ripe sporophyte; × 60. *D*. Open capsule, showing the two free valves; × about 16. *E*. Sections of two ripe spores and an elater; × about 300.

Fig. 6, *E*, shows the capsule of an older sporophyte. The apex forms a decided beak as it does in Blyttia. The sporogenous tissue does not yet show an evident difference between the future spore mother cells and the young elaters.

Somewhat later, some of the cells of the sporogenous tissue divide transversely into short rows of iso-diametric cells, the young spore mother-cells, while the others remain undivided and lengthening still more finally develop into the elaters. No spore mother cells were found in division, so that the details of spore division could not be studied.

The sporophyte, as it grows older, has the foot distinctly separated from the seta by an evident constriction (fig. 7, *C*). In this respect Podomitrium more nearly resembles Mörkia or Calycularia than it does a typical Blyttia, where a distinct foot is absent. In *Blyttia (Mittenia) Zollingeri*, however, a foot like that of Podomitrium occurs.

The capsule of the ripe sporophyte closely resembles that of Blyttia from which it differs mainly in the presence of an elaterophore. The latter structure is apparently better developed in *Podomitrium Malaccense* than it is in *P. Fhyllanthus* to judge from the figures of Andreas.[7] There is no doubt that in the former it originates from the sporogenous area much as it does in Aneura. The inner cells of the elaterophore are prolonged into slender processes, and these elongated cells resembled in form the elaters, but none of those that were examined showed the spiral thickenings characteristic of the true elaters.

The outer layer of cells, forming the wall of the capsule, have their cell-walls uniformly thickened as in Blyttia.

The ripe spores are about 15 μ to 17.5 μ in diameter. The outer membrane is marked by fine reticulations, thus very much resembling the spores of *Blyttia radiculosa*, whose spores are almost identical in appearance with those of *Podomitrium Malaccense* except that they are slightly smaller. According to both Andreas[8] and Cavers[9] the sporogonium of *P. Phyllanthus* opens by four longitudinal slits as it does in Blyttia; but all of the open sporogonia of *P. Malaccense* seen by the writer showed two broad valves completely separated at the top (fig. 7, *D*), resembling in this respect *Calycularia radiculosa* or Mörkia. It may be that an examination of a larger number of specimens might show some variation in the mode of dehiscence.

Comparing *Podomitrium Malaccense* with other Anacrogynae, it is evident that it comes nearest to Blyttia, from which it differs, however, in the position of the reproductive organs, the presence of a definite foot in the sporophyte, and in the presence of a distinct elaterophore, as well as a different method of dehiscence.

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[7] Andreas, J. Ueber den Bau der Wand und die Oeffnungsweise des Lebermoossporogons. Flora **86**: 1899.

[8] Andreas, loc. cit.

[9] Cavers, The Inter-relationships of the Bryophyta—reprint from New Phytologist. 1911.

A comparison of the genera included in the families Aneuraceae and Blyttiaceae, viz., Metzgeria, Aneura, Umbraculum, Podomitrium, Calycularia, Mörkia, Makinoa, Symphyogyna and Blyttia, shows that there are no constant features which can be used certainly to distinguish the two families from each other; it will probably be better, as Cavers has suggested, to combine the two families into a single one.